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Abstract: Assuming that the acquisition and retention of memories have costs, properties of memories should fit the functional requirements for the system of memory. Based on a functional analysis of what path integration is meant to do, we predicted that odometric memories in desert ants should show (1) little improvement with repeated training: performance should be as good after one training trial as after six training trials, (2) decay of memory after 24 h, and (3) performance based solely on the most recent outbound trip, with no integration over multiple memories. Desert ants (Cataglyphis fortis) traveled in narrow straight plastic channels to forage for cookie crumbs in a feeder at 6- or 12-m distance. Each ant was tested once by being taken from the feeder and released 2 m from the end of a 32-m channel to run home. The distance at which the ant first turned back (first turn) constituted the data. In acquisition, groups trained one or six times before being tested had unsystematic scatter that did not differ significantly. In retention, ants tested after a 24-h delay showed larger unsystematic scatter than control animals tested after no delay. In integration, ants were trained five times at 6 or 12 m and then tested at 12 or 6 m, respectively. No evidence of integration of multiple odometric memories was found. The results show that the properties of odometric memories are indeed tailored to what the memory system is used for

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Assuming that the acquisition and retention of memories have costs, properties of memories should fit the functional requirements for the system of memory. Based on a functional analysis of what path integration is meant to do, we predicted that odometric memories in desert ants should show (1) little improvement with repeated training: performance should be as good after one training trial as after six training trials, (2) decay of memory after 24 h, and (3) performance based solely on the most recent outbound trip, with no integration over multiple memories. Desert ants (*Cataglyphis fortis*) traveled in narrow straight plastic channels to forage for cookie crumbs in a feeder at 6- or 12-m distance. Each ant was tested once by being taken from the feeder and released 2 m from the end of a 32-m channel to run home. The distance at which the ant first turned back (first turn) constituted the data. In acquisition, groups trained one or six times before being tested had unsystematic scatter that did not differ significantly. In retention, ants tested after a 24-h delay showed larger unsystematic scatter than control animals tested after no delay. In integration, ants were trained five times at 6 or 12 m and then tested at 12 or 6 m, respectively. No evidence of integration of multiple odometric memories was found. The results show that the properties of odometric memories are indeed tailored to what the memory system is used for. *Key words:* acquisition, desert ants, integration, memory, odometry, retention. *[Behav Ecol 17:227–235 (2006)]*

Navigation is essential for survival in central place foraging arthropods such as crabs, bees, and ants. The foraging animal must return home at the appropriate time, when food has been found or when danger threatens. A suite of coordinated behaviors is used in homing (Cheng, in press; Wehner, 1992; Wehner and Srinivasan, 2003). Desert ants of the genus *Cataglyphis* rely on both path integration and landmark-based route navigation (Wehner, 2003). They do not lay down or use any pheromone trails (Wehner R and Wehner S, 1986), the climate being too hot for volatile chemicals. In the much studied path integration system of *Cataglyphis*, the ant keeps track of the distance and direction to home as it travels, even in the third dimension (Wohlgemuth et al., 2001), and heads directly home at the opportune moment. The ant relies on a sky compass, based on the pattern of polarized light in the sky, to tell directions (Wehner, 1994, 2003). How ants estimate distance traveled, the problem of odometry, has yet to be unraveled. In flying honeybees, optic flow plays a major role in odometry (Srinivasan et al., 1997; Wehner and Srinivasan, 2003). Bees estimate the distance that they have flown chiefly by the amount of visual texture that has streamed past their eyes as they fly. In *Cataglyphis*, however, optic flow plays only a minor role (Ronacher and Wehner, 1995; Ronacher et al., 2000). Some other mechanism(s), probably involving proprioceptors, is perhaps used for odometry as well (Ronacher et al., 2000).

For ants whose nest is on the open salt pan, far from plants (potential landmarks), path integration is the chief homing mechanism. The journey home has two parts. A more or less straight leg home, the global vector, is based on the computed distance and direction from the ant's location at the start of the homing journey to its home. Because path integration is rarely accurate enough to pinpoint the home location, the global vector is complemented by a search pattern (Wehner and Srinivasan, 1981; Wehner R and Wehner S, 1986). The ant makes a sharp turn at the end of its global vector and begins to search in loops of ever-increasing size, frequently returning to the starting point of its search. These frequent returns necessitate the use of path integration during the search pattern as well. Functionally, this pattern is close to optimal for a searcher that might miss the nest even when passing close to it (Wehner and Srinivasan, 1981).

Experiments on odometry are usually conducted in narrow channels that essentially limit the ants' movement to one dimension, a technique introduced by Wehner R and Wehner S (1986: see Figure 1 for an illustration). The nest is surrounded by retaining walls, so that foragers are forced to travel down the channel, arriving at the end of the channel to a feeder. In parallel channels, the ant, with a bit of food in its mandibles, can be allowed to run home (training) or tested in a long channel. Optic flow under the ant, in the form of a textured pattern moving at different velocities under a transparent surface on which the ants travel, affects odometric estimates to a small but significant extent (Ronacher and Wehner, 1995). Optic flow to the sides, on the other hand, plays no role in odometry (Ronacher et al., 2000). Cheng and Wehner (2002) trained ants for five trials with systematic displacements before the homing journey (e.g., 6 m outbound, but 12 m homebound). The ants' odometric estimates of the distance home did not change, but search patterns were systematically affected in accord with the learning experience. The search tended to drift gradually away from the start of the homebound run.

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In the work reported here, we tested some functional predictions concerning the acquisition, retention, and integration of odometric memories in *Cataglyphis*. Assuming that the acquisition and retention of memory have costs (Dukas, 1999), memory systems ought to fit approximately what the memory is required for and not be "too good" or insufficient.

The foraging behavior of a closely related desert ant in the Tunisian salt pans, *Cataglyphis bicolor*, has been amply documented (Wehner et al., 1983), and this descriptive work forms the basis for predictions. Ants forage individually, with each forager typically heading off from the nest in roughly the same direction on each trip, a phenomenon called sector fidelity. Over successive journeys, ants tend to forage farther and farther from their nest. *C. bicolor* forages mostly (90% of the searching) within ~32 m of its nest (Wehner et al., 1983), but *Cataglyphis fortis* travels up to 100–200 m from its nest (Wehner R and Wehner S, 1986). Each trip is distinct, even when the ant is repeatedly attracted to an experimentally placed feeder (Wehner et al., 1983: Figures 19 and 20). Without experimental intervention, however, prey are scattered, consisting mostly (>80% by frequency) of other arthropods that have died. Run duration on a foraging trip averages 52.9 min (SD 3.9 min), with a forager making an average of 4.2 trips per day (SD 0.3 trips). While *Cataglyphis* ants are highly thermophilic (Wehner et al., 1992), durations of runs are limited by the process of desiccation. On the hottest days at our field site, with maximum temperature of ~45°C, *C. fortis* ants die of desiccation within 2 h (Wehner R and Wehner S, unpublished data). Thus, twice that time, or 4 h, might be a generous estimate of the maximum duration that an ant can forage in the open on one trip during the active summer period.

In light of this natural history, we hypothesize that the memory for the vector derived from path integration on each foraging trip is systematically erased when the ant arrives home. These "old" memories can only serve to interfere with path integration on the unique current trip. This leads to the prediction that in acquisition, repeated training with one particular outbound distance should not improve performance, the odometric memory being based on the most recent outbound journey and not on the average of past journeys. Although the process of estimating each single outbound journey might improve with practice, we predict that this effect would be small. An ant needs to be good enough to get home on its first foraging trip. We compared ants with one and six training trials at one outbound distance and predicted no systematic differences in unsystematic scatter in the ants' odometric estimates.

Ziegler and Wehner (1997) tested the retention of odometric memories in *C. fortis*. Ants were allowed to forage repeatedly in a 12-m channel originally used by Wehner R and Wehner S (1986: Figure 10) and different in construction from what we used. They report a halving of accuracy with 2 days delay. As reviewed, in normal foraging, ants neither follow the same route nor reach the same food location repeatedly. We thus tested ants' retention with only a single outbound trip. Given that ants cannot survive for a day in the open, we predicted a significant decay in odometric memory after a 24-h delay. Ants were tested with various delays, but we explicitly compared ants with a 24-h delay against controls tested with no delay.

Integration means pooling past experiences. In many systems of memory, memory is formed by pooling many previous experiences. In estimating distance traveled on an outbound journey, however, integration should not take place at all. Again, because every journey is different, odometric memory should be based solely on the most recent experience, the current outbound trip. We tested integration by training ants to travel one outbound distance for five trips and then either doubled or halved the outbound distance on the sixth trip. Ants were tested either immediately after the sixth outbound trip or after a 24-h delay. A lack of integration means that the return distance should not be affected by the five previous training trials. We compared ants in this experiment with ants from the zero-delay group in the retention experiment and predicted similar estimates of the homebound distance.

METHODS

Setup and animals

We conducted the study on a single nest of *C. fortis* in the salt pans near Maharès, Tunisia, from June to August 2004. A rectangular plastic frame measuring 75 × 45 cm (outer dimensions) surrounded the nest (Figure 1). The frame consisted of 10-cm plastic channels (the same kind used for the channels) and had three slots on one side to which three parallel plastic training channels were connected. Sliding gates in the slots were used to control the ants' entry and exit from the nest. Two of the channels were outbound channels 6 and 12 m in length. The third channel was an inbound channel whose length we altered to 6 or 12 m based on the experimental condition. At the end of each outbound channel was a feeder sunk in the ground, coated with fluon to prevent ants from escaping. We provisioned each feeder with crumbs of cookies (Saida brand). We placed a 32-m test channel parallel to the training channels. The channels were constructed with 1-m segments, each with a connecting piece at one end slightly bigger than the segment. We joined segments by using nuts and bolts. Ants could exit from their nest when the sliding gate for the outbound channel was lifted and they had to travel the length of the channel to get to the feeder.

General procedure

We marked experimental ants that were trained to go back to their nest in the inbound channel, after they first arrived at

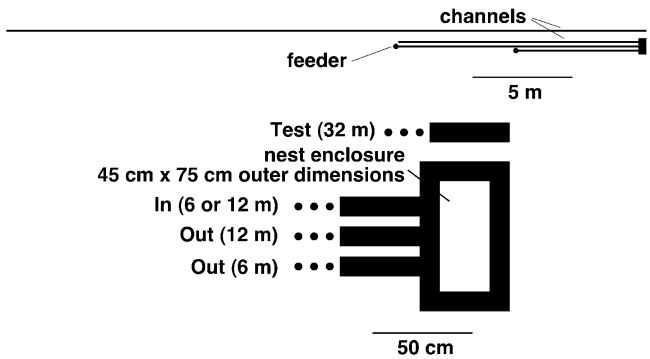

Figure 1
Experimental apparatus. Top. The training setup consisted of two outbound channels 6 and 12 m in length and an inbound channel 12 m in length. At the left end of each outbound channel was a dish with crumbs of cookies (feeder), sunk into the ground, so that ants arriving at the end of the outbound channel fell into it. On training trials, the ants returned to the nest in the inbound channel. The 32-m-long test channel was a separate channel parallel to the training setup, used only for tests. Bottom. A magnified view of the right end of the apparatus. The nest enclosure to the right of the inbound and outbound channels surrounded the nest. It was constructed by interconnecting channel pieces (all 10 cm wide and 10 cm tall). Plastic gates between the enclosure and the channels allowed experimental control over entry and exit between the channels and the nest.

the feeder and picked up a piece of cookie. We marked ants that were tested without training after the test (to ensure that they were not used again in any experiment). Each trial was either a training trial or a test. We trained and tested ants individually. On a training trial, we released the ant with its crumb of cookie in the inbound channel, the same distance from the nest as the outbound distance. We opened the gate to the nest at the end of the inbound channel when the ant neared it. On a test, we picked up the ant within 2 min of its arrival at the feeder (so that delays due to experimental handling was minimal). We transferred it in the dark to the test channel and released it 2 m from the far end to run home with its cookie. The dependent variable was the distance from the release point in the test channel to the point of the ant's first turn. The first turn was the point at which the ant first turned back and walked at least 20 cm, a standard measure from past studies (Cheng and Wehner, 2002; Ronacher et al., 2000; Sommer and Wehner, 2004). We measured first turns to the nearest 0.1 m according to a measuring tape beside the test channel. We gave ants that started off in the direction away from the nest a first turn of 0 m and those that did not turn (ran the length of the channel) a score of 30 m.

Experiment 1: acquisition

In Experiment 1, we questioned whether ants get better in estimating distances with experience at the same outbound distance. We assigned ants at random to two groups, one trained with the 6-m outbound distance and the other with the 12-m outbound distance. Within each of these groups, we trained one batch of ants just once to the feeder, while the other batch had six training trials to the same distance ($n = 20$ per group). The ants in the one-trial group were released in the inbound channel (with a piece of cookie) after their first arrival; this constituted a training trial. The next time they arrived at the feeder, they were tested. The ants in the six-trial group were tested on the seventh trip to the feeder, after six training trials. We also tested some ants ($n = 12$ per group) with zero trials of training (i.e., on their first arrival at the feeder). But for formal statistical comparisons, we did not include these ants because on first encountering the channel, an ant typically wandered back and forth many times before finally landing in the feeder. This increased the accumulation of errors in the odometric estimate of the outbound trip. On their second and subsequent outbound trips, ants usually moved directly to the feeder.

Experiment 2: retention

In Experiment 2, we determined how the ants' estimate of distance traveled decays with the passage of time. We opened the gates for both the 6-m and the 12-m outbound channels and allowed ants to choose an exit. We tested ants that came to the feeder and picked up a piece of cookie either immediately or after 3-, 24-, 48-, 96-, or 192-h delays ($n = 24$ per group). During the delay, we held ants captive in containers in natural light conditions and provided them with air, food, and moisture. The mortality rate in captivity was 5%. We recorded first turns on tests.

Experiment 3: integration

In Experiment 3, we determined whether ants integrate previous trips with the current outbound trip in estimating outbound distances, both immediately and after a 24-h delay ($n = 20$ per group). We trained ants for five training trials to one particular distance (6 or 12 m), and on the sixth trial (a test), we either doubled the outbound distance (from 6 to 12 m; the 6–12 groups) or halved it (from 12 to 6 m; the 12–6 groups). We tested ants that arrived at the feeder and picked up a piece of cookie either immediately or after a delay of 24 h and recorded their first turns in the test channel.

Analysis

We compared means and variances of first turns in each experiment. Because of the possibility of heterogeneity in variance, we compared means with Welch's ANOVA using JMP (SAS, 2002). Use of nonparametric tests to compare means, Kruskal-Wallis (for three or more groups) or Mann-Whitney U test (for two groups), led to the same pattern of inferential statistics. We compared variances across groups by the test of O'Brien (1979) using JMP. We chose this test because it is more robust against the effects of outliers than traditional tests such as Bartlett's or the F_{max} test. Odometric data in our test species frequently include outliers. The use of another test robust against the effects of outliers, the Brown-Forsythe test (Brown and Forsythe, 1974) in JMP, produced the same pattern of inferential statistics on variances. In *C. fortis*, interindividual variation in odometric estimates increases with the mean distance to estimate (Sommer and Wehner, 2004). In each experiment, we compared SDs relative to means or coefficients of variation (CVs). This meant dividing each first turn by the mean of the group in question and then comparing the variances across groups. We justify this choice in the results. We analyzed the groups with the 6- and 12-m outbound training distances separately with alpha set at 0.05.

RESULTS

Descriptive data: comparing the 6- and 12-m outbound distances

Table 1 lists key descriptive data for all experiments. The first question for data analysis was how to compare variances across groups within each experiment. To do this, we compared performance at the 6- and 12-m training distances in four conditions with immediate testing—acquisition: one-trial training and six-trial training; retention: 0-h delay; integration: immediate tests. Table 1 shows that the CVs (SD/M) are similar in the 6- and 12-m groups. We divided each first turn by the mean of the group and compared the variances of CVs of the 6- and 12-m groups in each of the four conditions listed above. In no case did the variances differ significantly by O'Brien's test. On average, the CV for the 6-m groups was 0.20; for the 12-m groups, it was 0.19. Thus, SD scales with the mean in interindividual odometric estimates, a form of Weber's law (Cheng et al., 1999). We thus divided the first turn by the mean of each group (the measure CV) before comparing variances across groups in each experiment.

Experiment 1: acquisition

We tested ants after one or six training trials in the channel (Figure 1). Ants with one training trial had a higher mean first-turn distance and numerically larger variances compared with ants with six training trials (Figure 2 and Table 1). For the 6-m groups, the distance at first turn differed as a function of number of training trials (Welch's ANOVA $F(1,33.7) = 8.07$, $p = .008$), whereas unsystematic scatter (CV) did not (O'Brien's $F(1,38) = 1.43$, $p = .239$). For the 12-m groups as well, the distance at first turn differed between ants trained one and six times (Welch's ANOVA $F(1,28.7) = 4.51$, $p = .042$), while unsystematic scatter (CV) did not (O'Brien's

Table 1
Summary data for the three experiments (in meters)

Outbound distance (m)	Experiment	Condition (*n*)	Mean (M)	SD	CV (SD/M)	75th percentile	Median	25th percentile
		Number of training trials						
6	Acquisition	Zero-trial (12)	7.0	1.19	0.17	8.1	7.0	6.2
		One-trial (20)	7.8	1.24	0.16	8.7	7.7	7.0
		Six-trial (20)	6.8	0.86	0.13	7.5	6.9	6.3
12	Acquisition	Zero-trial (12)	12.8	4.84	0.38	15.6	13.8	8.5
		One-trial (20)	15.0	3.68	0.24	16.4	15.1	11.8
		Six-trial (20)	13.1	1.92	0.15	14.3	12.9	11.5
		Delay interval						
6	Retention	0 h (24)	7.3	2.77	0.38	7.5	6.6	6.0
		3 h (24)	6.7	1.88	0.28	7.6	6.6	5.7
		24 h (24)	6.9	4.32	0.62	10.3	6.6	3.3
		48 h (24)	6.9	3.80	0.55	8.2	6.5	4.4
		96 h (24)	8.0	5.07	0.64	10.2	8.4	5.5
		192 h (24)	3.1	4.36	1.41	4.4	1.1	0.2
12	Retention	0 h (24)	11.9	2.53	0.21	13.3	11.9	10.7
		3 h (24)	12.5	3.20	0.26	13.7	12.7	10.8
		24 h (24)	12.4	4.17	0.34	16.1	12.8	8.3
		48 h (24)	8.8	4.74	0.54	12.2	8.0	6.8
		96 h (24)	9.3	5.93	0.64	11.2	8.2	6.1
		192 h (24)	2.9	2.61	0.89	4.4	3.0	0.4
12–6	Integration	0 h (20)	7.2	1.06	0.15	7.8	7.0	6.5
		24 h (20)	27.8	5.78	0.21	30.0	30.0	30.0
6–12	Integration	0 h (20)	11.3	1.82	0.16	12.1	11.4	10.0
		24 h (20)	27.5	6.18	0.22	30.0	30.0	28.6

The dependent variable is the distance at first turn on a test, which is the distance that the ant traveled in the test channel before turning back and moving for at least 20 cm. CV stands for coefficient of variation. In the acquisition experiments, ants were trained for different numbers of return trips before being tested in the test channel. In the retention experiments, ants were captured on their first outbound trip and held for various delay intervals before being tested. In the integration experiments, ants made five return trips at one outbound distance (6 or 12 m) and then traveled a different outbound distance (12 or 6 m) on their last outbound trip before being tested in the test channel, either immediately or after a 24-h delay.

$F(1,38) = 2.89$, $p = .097$). We tested some ants with no training as well, immediately after they arrived at the feeder for the first time. We did not compare these ants formally with the one-trial and six-trial ants because on the first trip to the feeder, the ants typically wandered back and forth in the channel many times before arriving at the feeder. But the descriptive data for this group (Table 1) show that their first turns were similar in distance to those of ants trained six times.

Experiment 2: retention

We captured ants after their first arrival at the feeder (at 6 or 12 m for different groups) and retained them for different amounts of time. The results (Figure 3 and Table 1) show that with increasing delay, distance at first turn decreased while unsystematic scatter increased. For the 6-m groups, distance at first turn differed across delays (Welch's ANOVA $F(5,62.7) = 3.68$, $p = .006$) as did unsystematic scatter (CV, O'Brien's

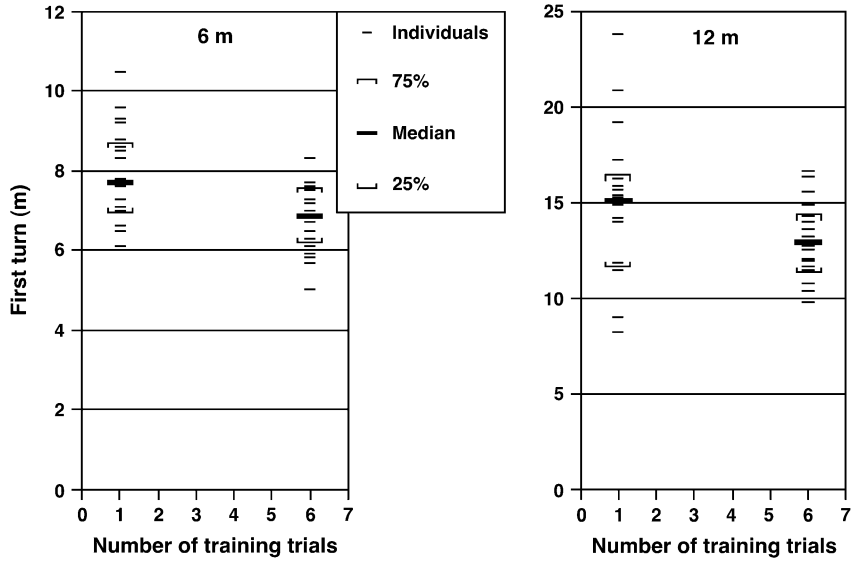

Figure 2
Data from acquisition experiment at the 6- and 12-m outbound distances. Individual first turns are shown, along with medians and quartiles.

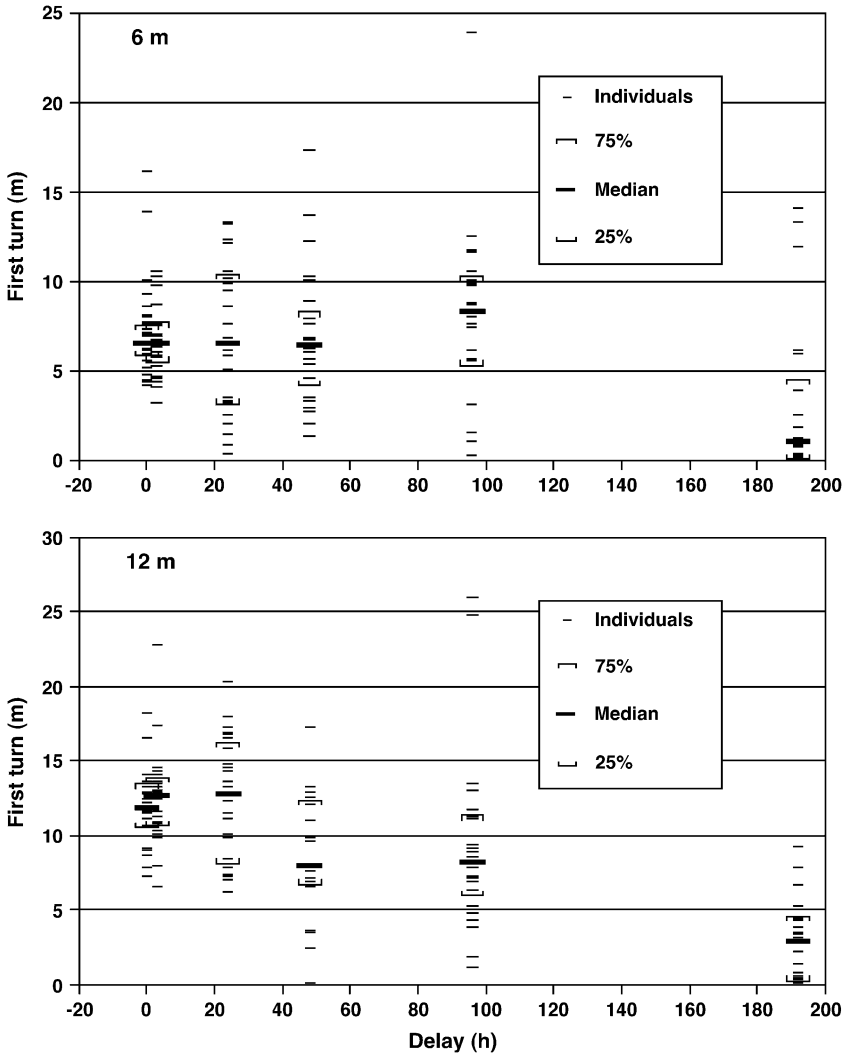

Figure 3
Data from retention experiment at the 6- and 12-m outbound distances. Individual first turns are shown, along with medians and quartiles.

$F(5,138) = 4.94$, $p < .001$). For the 12-m groups as well, the distance at first turn differed across delays (Welch's ANOVA $F(5,63.6) = 39.74$, $p < .001$) as did unsystematic error (O'Brien's $F(5,138) = 5.32$, $p < .001$). The drop in mean first-turn distance occurred at 8 days delay for the 6-m groups and at 2 days delay for the 12-m groups. In unsystematic scatter (CV, Table 1), we then compared groups having 0- and 24-h delays, applying O'Brien's test on just the two groups. For both outbound distances, ants with a 24-h delay had larger unsystematic scatter than ants with no delay (6 m: O'Brien's $F(1,46) = 6.27$, $p = .016$; 12 m: O'Brien's $F(1,46) = 6.81$, $p = .012$). Comparing ants with 0- and 3-h delays revealed no significant differences in unsystematic error at either distance (6 m: O'Brien's $F(1,46) = 0.72$, $p = .403$; 12 m: O'Brien's $F(1,46) = 0.36$, $p = .554$).

Experiment 3: integration

We trained some ants five times to travel 6 m to the feeder and then tested them after a 12-m outbound trip, either immediately or after a 24-h delay (groups 6–12). We trained other ants five times to travel 12 m to the feeder and then tested them after a 6-m outbound trip, again either immediately or after a 24-h delay (groups 12–6). Ants tested immediately had similar first-turn distances as ants from the retention experiment that were tested immediately (Ret 0; Figure 4). Ants tested after a 24-h delay, however, mostly ran the length of the test channel (30 m; Figure 4). Only one ant in each group ran less than 21 m before turning. No ant traveled between 6 and 12 m before turning. We further tested some animals after a 24-h delay in 50-m channels (results not presented). Most of those also ran the length of the channel.

We first compared the ants tested immediately with Ret 0 ants from the retention experiments. For the 12–6 group and its corresponding Ret 0 group, distance at first turn did not differ significantly (Welch's ANOVA $F(1,30.7) = 0.06$, $p = .814$) and unsystematic scatter (CV) did not differ significantly (O'Brien's $F(1,42) = 2.35$, $p = .132$). For the 6–12 groups and its corresponding Ret 0 group as well, distance at first turn did not differ significantly (Welch's ANOVA $F(1,41.2) = 0.85$, $p = .362$) and unsystematic error did not differ significantly (O'Brien's $F(1,42) = 1.08$, $p = .305$). The lack of significant differences in distance at first turn means that the five trials of training at a different distance did not affect odometric estimates, indicating a lack of integration in the immediately tested animals.

We then compared ants tested after a 24-h delay with ants tested immediately. For the 12–6 groups, ants with a 24-h delay had longer distances at first turn (Welch's ANOVA $F(1,20.3) = 246.88$, $p < .001$), but CVs did not differ significantly between groups (O'Brien's $F(1,38) = 0.36$, $p = .550$). For the 6–12 groups as well, ants with a 24-h delay had longer distances at

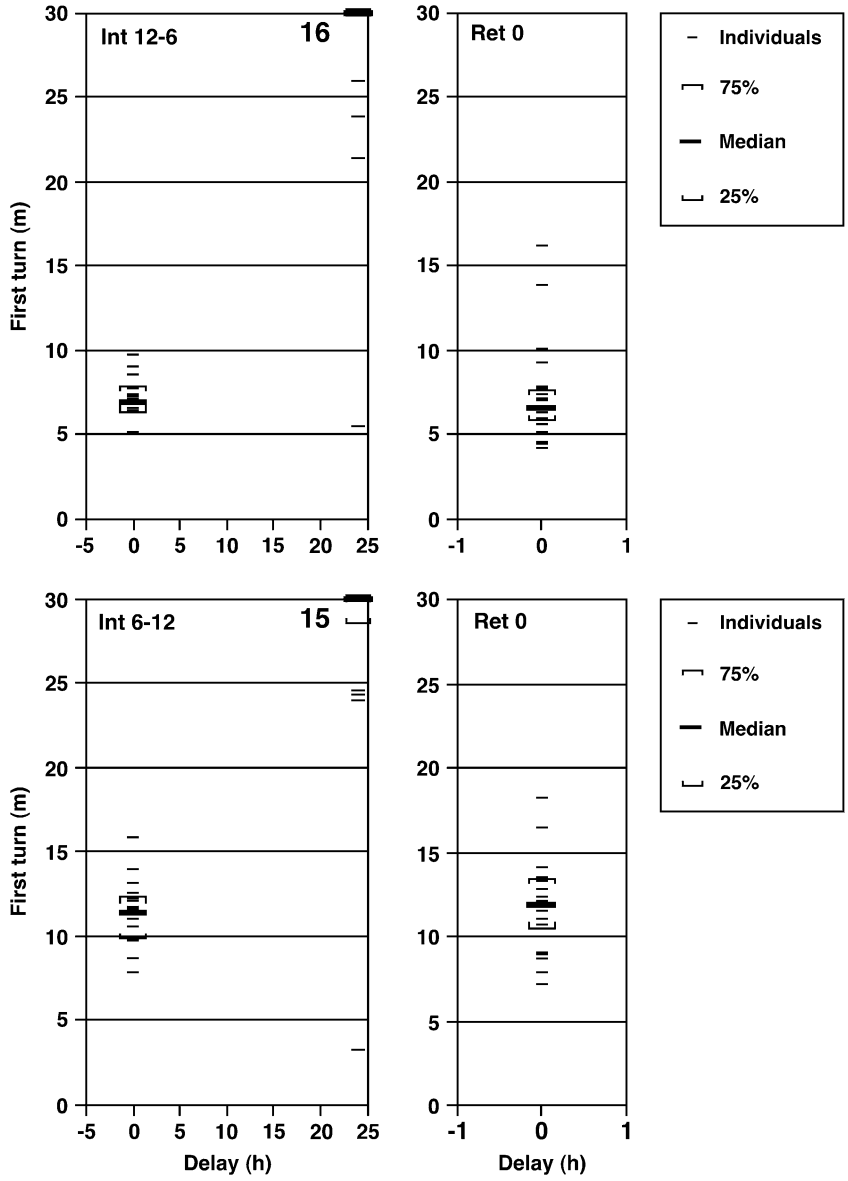

Figure 4
Data from integration experiment for ants trained five times at the 12-m outbound distance and then tested after a 6-m outbound trip (Int 12–6) and ants trained five times at the 6-m outbound distance and then tested after a 12-m outbound trip (Int 6–12). Individual first turns are shown, along with medians and quartiles. The data from the retention experiment, 0-h delay, are shown on the right. The number in the top right corner of the top left panel indicates that 16 ants traveled 30 m to the end of the test channel without turning. Likewise, the number in the top right corner of the bottom left panel indicates that 15 ants traveled 30 m to the end of the test channel without turning. In both these cases, individual data points at 30 m are not visible because the median is at 30 m.

first turn (Welch's ANOVA $F(1,22.2) = 126.25$, $p < .001$), but CVs did not differ significantly between groups (O'Brien's $F(1,38) = 0.33$, $p = .567$). This implies that ants tested after a 24-h delay overestimated the outbound distance compared to ants tested immediately. Note, however, that variances in the groups tested with a 24-h delay were artifactually reduced because the maximum distance was capped at 30 m.

DISCUSSION

The results on the whole support the predictions made on functional grounds. No significant effect of number of training trials on unsystematic scatter was found, decay in odometric memory was found after a 1-day delay, and no evidence for integration of odometric memories over multiple outbound journeys was found.

The prediction for acquisition is that unsystematic error would not show a reduction between one and six trials of training. In the acquisition experiment, the number of training trials did not affect unsystematic scatter at either training distance. But numerically, unsystematic error was smaller with six training trials, especially for the 12-m training distance (Table 1). This may reflect some improvement over trials in estimating distance traveled in the channel. It is unlikely to reflect an averaging of the estimated outbound distances on multiple trips because Experiment 3 found no evidence for such integration. The acquisition experiment did reveal a difference in mean estimates of distance traveled as a function of number of training trials, with one-trial ants running farther than six-trial ants, the difference being significant at both training distances. Ants with no training that were tested immediately (from the acquisition and retention experiments) performed like the six-trial ants (Table 1). Overestimation of distances is sometimes found in *C. fortis* (e.g., Cheng and Wehner, 2002). We have no plausible explanation for why ants with one trial of training would run farther than ants with zero and six trials of training. Such a pattern might be the result of sampling error.

Regarding retention, we predicted that odometric memory would deteriorate after 24 h. This is because an ant cannot survive that long in the open in the desert heat. The data show a significant increase in unsystematic scatter at 24-h delay for

both training distances, while the average distance at first turn remained similar to those of ants tested with no delay (Figure 3). The similarity in mean odometric estimates gives some confidence that the ants were attempting to use their odometric memory, while the increase in scatter indicates a decay in the memory. Because the pattern of unsystematic scatter seems to differ for the two training distances, we did not fit any curves to the scatter as a function of delay. The distance traveled by the ants before turning differed as a function of delay. At 8 days delay, many ants did not run very far before turning (Figure 3). A reasonable interpretation is that these ants had abandoned any attempt to path integrate and were engaging in search behavior from the start of the test. In that case, such an ant would attempt to turn in loops (Wehner and Srinivasan, 1981), and this would result in turning back after short distances in the channel. The data are similar to those obtained by Ziegler and Wehner (1997) using channels of different construction and repeated training of the ants at the 12-m training distance. These authors also found increasing unsystematic scatter with delay, with a substantial increase at 2 days and a drop in mean distance of first turn at 8 days delay. A 24-h delay, however, was not tested.

Concerning integration, we predicted no integration: the ants should rely solely on the most recent outbound trip. In the integration experiment, the prediction translates to similar distances at first turn in ants tested immediately and after a 24-h delay, with both conditions similar to control ants that had no conflicting training with an outbound distance that differed from the outbound distance on the test. With the immediate test in the integration experiment, the prediction was confirmed (Figure 4). Using a different setup with channels and landmarks, Collett et al. (2003a) also found that path integration, on immediate testing, was based on the most recent outbound trip and not on experience gathered from previous trips. With the test at 24-h delay, our prediction was disconfirmed (Figure 4). Most of the ants ran the length of the channel, never turning back. This pattern of behavior, however, also does not support the integration of odometric memories. In integrating odometric memories, the ants should average the most recent odometric memory with earlier odometric memories. For both conditions (6–12 and 12–6), this means a distance somewhere between 6 and 12 m. No ant did this; most ants ran much farther than 12 m.

How might we interpret this behavior? The behavior is based on a combination of training with multiple trials and delay in testing. Ants trained multiple times but tested immediately (in the acquisition and integration experiments, Figures 2 and 4) did not do this. Ants without training, but tested at delays up to 8 days (retention experiment, Figure 3) also did not do this. After a 24-h delay, ants might have switched from path integration to route-based behavior. In the context of being in the channel with the motivation to home, they head in the appropriate direction in the channel until they run into the enclosure around the nest. After all, this was what happened on every training trial. This form of context-triggered route-based behavior has been found in this species (Collett et al., 1998; Collett et al., 2001) and others (Collett et al., 2003b; Graham and Collett, 2002). We suppose that after learning this route-based behavior and after a delay at which odometric memory deteriorates, the ants prefer to rely on the route-based strategy. In case they forage repeatedly at the same site, the route-based strategy is what the ants learn to use, not the averaging of the vectors of multiple outbound trips.

The data of Ziegler and Wehner (1997) data are against this hypothesis. In their retention experiments, ants were trained repeatedly in the training channel. But their ants, of the same species, did not overshoot at any delay. Supporting this hypothesis are our recent as yet unpublished data from another formicine desert ant, the Central Australian *Melophorus bagoti*, which usually follow stereotypic routes (Kohler and Wehner, 2005). They were tested in channels of the same construction as those reported in this article. Repeated training sometimes led to overestimations of distance traveled, even when tested at the same outbound distance as in training. As mentioned, the channels of Ziegler and Wehner (1997) were different from those that we used. Perhaps the nature of the channel matters. Further research is needed to resolve this issue.

The lack of integration of odometric memories in *Cataglyphis* contrasts with other systems in which integration is found, especially after some delay since the most recent experience. On immediate testing, rodents' memory for the reward levels of foraging patches is based mostly on the most recent experience. But after some delay since the last foraging experience, decisions are based more on an average of all experiences (Devenport L and Devenport J, 1994; Devenport et al., 1997). Hence, the relative weighting for the most recent relevant experience decreases with the passage of time since the last experience. Weighting is time dependent and decays exponentially with elapsed time. Functionally, this form of time-dependent weighting may serve to tune the "integration window" to the most optimal width. When very little time has elapsed since the last relevant experience, the world is likely to continue as in the recent past, and a narrow integration window is optimal. But when a good deal of time has elapsed since the last relevant experience, the importance of the last experience for predicting future events diminishes, and the best estimate of conditions is provided by a broad sampling of many experiences, that is, from integrating over a wide window.

A form of time-dependent weighting may be occurring in our integration experiment as well. Based on Experiment 3, we suppose that odometric memory is based solely on the most recent outbound experience. Context-triggered route memories (Collett et al., 2003b), on the other hand, are based on past homebound journeys, necessarily further back in time. Immediate testing favors the most recent odometric memory, while delayed testing favors the past route memories, which outnumber the single current outbound experience. Although more work is required for confirmation, this pattern may reflect the choice on the part of the ant of the best memory for the navigational task, a form of optimal choice of strategy.

If our functional analysis of memory systems has merit, then there is no typical navigational memory system in desert ants. Systems of memory should show different properties based on the functions of the memory. Landmark memories, for example, would have different properties from odometric memories. Landmarks are stable over the short life of a foraging ant (unlike each outbound journey that forms the basis of odometric memories), favoring a system of memory with lifelong retention, as found by Ziegler and Wehner (1997). And because foraging locations normally vary, whereas the nest stays at a constant location, ants might be expected to learn landmarks around the nest better than landmarks around an experimentally provided feeding site, as found by Bisch-Knaden and Wehner (2003).

Looking beyond *Cataglyphis*, different systems of memory in general may have different properties in acquisition, retention, and integration, depending on what they were "designed to do." At the least we can point to differences in these properties across systems. In the voluminous literature on conditioning, for example, food conditioning in pigeons (autoshaping) shows gradual acquisition, slow decay in retention, and integration over multiple experiences (Gallistel and Gibbon, 2002). Food conditioning in honeybees (proboscis extension reflex), on the other hand, is rapid, occurring in

two trials (Menzel and Giurfa, 2001). Moreover, the system is "tuned" to particular conditioned stimuli, odors, and mechanical stimulation. All these properties make functional sense for a system geared to work when a bee lands on a flower in foraging. Aversive conditioning is typically acquired faster than food conditioning. In rats, fear conditioning can be established with one experience with electric shock (Isaacson and Wickelgren, 1962). Aversive taste conditioning in rats, in which a novel taste is followed by poison to make the animal sick, can also be rapid and is selectively tuned to taste stimuli rather than audiovisual stimuli (Garcia and Koelling, 1966).

Retention might also vary across memory systems. In the honeybee, Menzel and Giurfa (2001) proposed that distinct memory systems differing in durability, isolated in the lab from behavioral and physiological work (Menzel, 1999), are adapted for different components or tasks in foraging. In sticklebacks, the retention duration of foraging skills might be dependent on prey diversity. When prey diversity is high, the retention of foraging skills might interfere with learning to forage on new prey types. A population living in a freshwater pond with low prey diversity has longer retention of foraging skills than a population living in a marine environment with high prey diversity or one that moves between marine and freshwater environments, the latter being the same species as the freshwater population (Mackney and Hughes, 1995).

Integration over experiences might also be expected to show flexibility, depending on the nature of experiences. Thus, rats can learn to adjust how much experience to integrate (Gallistel et al., 2001). Under rapidly changing contingencies, they learn to adjust quickly to changing contingencies, thus integrating over a minimum number of experiences and being close to "ideal detectors" of change. The same species, under more stable conditions, are slow to react to changes in contingencies, showing integration over much past experience. A decay in weighting with time elapsed since the establishment of a memory (Devenport L and Devenport J, 1994; Devenport et al., 1997) might be expected to be a general principle. But this principle has been little tested and not at all on any invertebrate system of memory to our knowledge.

We do not mean to be Panglossian. Given our current lack of understanding of the neurobiological bases of memory, it is unclear how far functional analyses of memory can be pushed. But assuming that memory has costs (Dukas, 1999), it is reasonable to assume that evolution could fashion different systems of memory with different functional properties. In our study case of odometric memories in a desert ant, the functional predictions were confirmed on the whole. Repeated practice did not improve performance, memory decayed in a day, and no evidence of integration of multiple odometric memories was found. Ants tested with a delay in the integration experiment, however, might have switched from path integration to route-based behavior, thus exhibiting integration of two different navigational strategies.

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